
Brodiaea sierrae (Themidaceae), a New Species from the Sierra Nevada Foothills of California, U.S.A.

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ABSTRACT. *Brodiaea sierrae* (Themidaceae), a new diploid species from the Sierra Nevada foothills of California, U.S.A., is described and illustrated. Morphologically, it is most similar to the tetraploid *B. leptandra*, from which it differs by having larger flowers, with perianth lobes up to 40 mm long (vs. 20–30 mm). The new species is also morphologically similar to *B. californica* but differs by the staminode morphology and by the lack of anther appendages. Although morphology and other data support a close relationship between the three species, they are geographically and edaphically disjunct in northern California.

Key words: *Brodiaea*, California, Themidaceae.

The genus *Brodiaea* Smith (Themidaceae) consists of approximately 14 or 15 species, almost entirely restricted to the California Floristic Province (Niehaus, 1971, 1980; Keator, 1993; Pires, 2002). *Brodiaea* has a rich taxonomic history and has been placed variously in Liliaceae, Amaryllidaceae, and Alliaceae (Hoover, 1939; Keator, 1967, 1989; Niehaus, 1971, 1980). Recent phylogenetic studies, however, place *Brodiaea* and relatives not with *Allium* L. and Alliaceae but with Hyacinthaceae and other related monocot families (Fay & Chase, 1996; Fay et al., 2000; Pires et al., 2001; Pires & Sytsma, 2002). As a result, *Brodiaea* has been reassigned to the family Themidaceae or a more inclusive Asparagaceae (Angiosperm Phylogeny Group, 2003). These studies have focused on relationships among families and genera and have not addressed relationships within *Brodiaea*, which remain poorly resolved despite having been monographed twice (Hoover, 1939; Niehaus, 1971). The genus remains a nearly untapped source for investigations on edaphic relationships, polyploidy, and hybridization.

While investigating hybridization among *Brodiaea* species, I noticed that populations of *B. californica* Lindley growing sympatrically with hybridizing species occurred in two distinct forms correlated with substrate and elevation. Upon closer examination, morphological differences between the forms became apparent. The lower elevation form includes the type of *B. californica*. The higher elevation form, which is

significantly different from *B. californica* and morphologically more similar to *B. leptandra* (Greene) Baker, is described herein as a new species.

Brodiaea sierrae R. E. Preston, sp. nov. TYPE: U.S.A. California: Butte Co., 2.1 km W of Hurleton, along Forbestown Road, 19 June 2004, R. E. Preston 2261 (holotype, DAV; isotypes, JEPS, K, MO, NY, RSA, US). Figures 1, 2.

Haec species pulchra, in California ad infimos montes Sierra Nevada septentrionalis indigena, a subsp. *leptandra* floribus majoribus et stylis longioribus differt, et a subsp. *californica* marginibus staminodiorum integris et appendicibus antheris destitutis differt.

Corm with coarse fibrous coat, 1.5–3 dm below ground level; leaves lunate in cross-section. Scape stout, 2–8 dm tall, pedicels (0–)1.5–8.5(–16) cm long; inflorescence an umbel. Perianth 33–52.5 mm long, rose-violet to blue-violet, tube (8–)8.5–14(–15.5) mm long, lobes (24–)25–38(–40) mm long, inner (6–)6.5–11(–12) mm wide, outer (4–)4.5–7.5(–8.5) mm wide, ascending, recurved; staminode (20–)20.5–30(–31) mm long, white, linear, erect and approximate to stamens, recurved near the tip but not narrowed, margin entire, one-quarter involute, midrib noticeably thickened; stamens (12–)17–26.5(–28) mm long, filaments (7.5–)9–14.5(–15) mm long, dilated at base, anthers 10–15(–16.5) mm long, linear, apices of anther lobes erect with slight notch between; ovary ovoid, 6–10(–11) mm long, style 20–31(–34.5) mm long, ovules (12 to)17 to 36(to 42). Perianth tube in fruit translucent and splitting; fruit a loculicidal capsule; seeds black, ovoid to rhomboid, 3 mm long, margins prominently ridged. Chromosome number $n = 6$ (Niehaus, 1971, based on *Niehaus 245* [UC], 543 [UC]).

Phenology. *Brodiaea sierrae* blooms in June and July.

Distribution and ecology. *Brodiaea sierrae* is endemic to the Sierra Nevada foothills of Butte, Yuba, and Nevada Counties in California, with all but one documented population lying in a narrow elevation band between 320 and 945 m (Figure 2). The

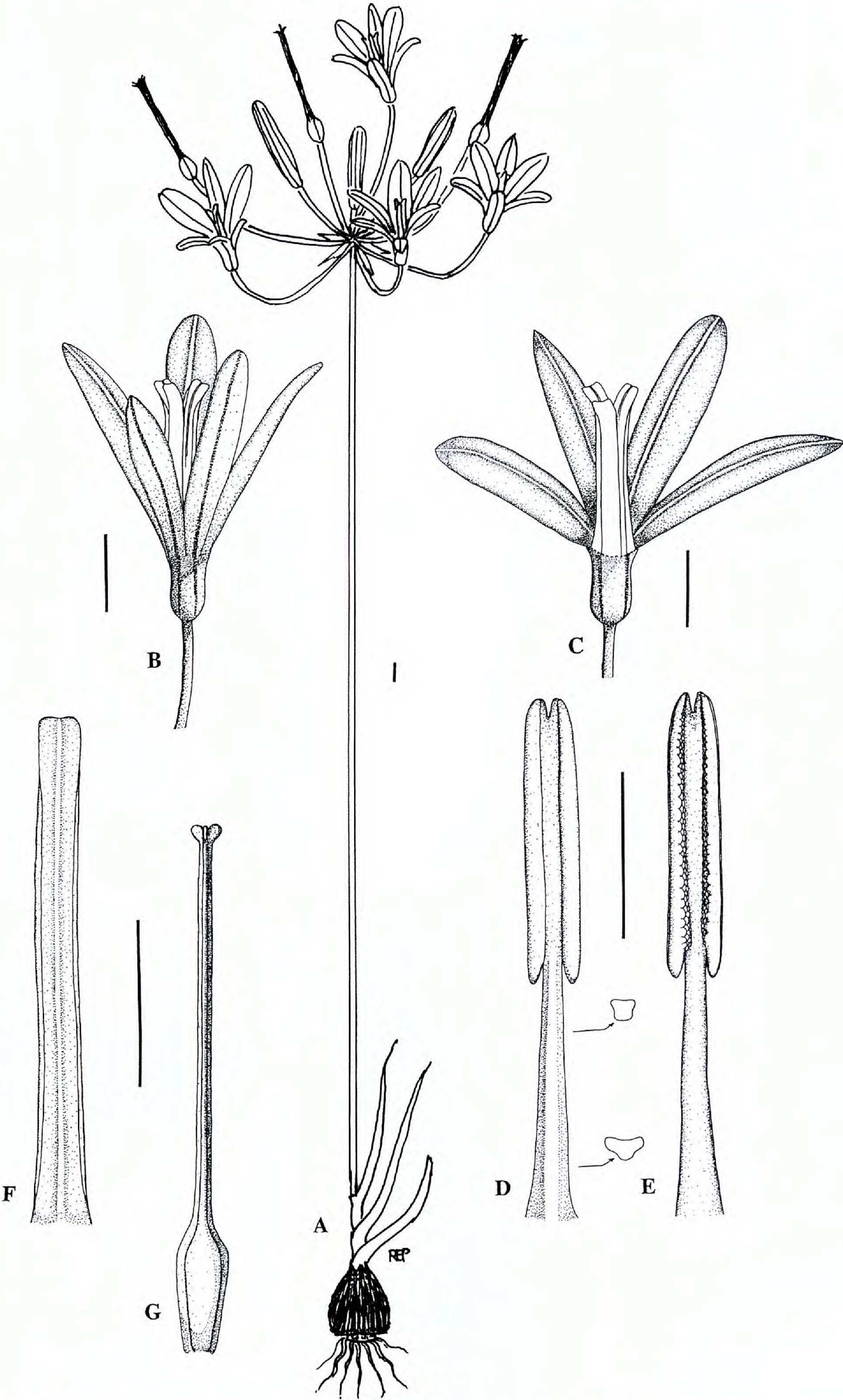


Figure 1. *Brodiaea sierrae*. —A. Habit. —B. Lateral view of flower. —C. Perianth, with 2 lobes removed to show position of staminodes. —D. Stamen (adaxial view). —E. Stamen (abaxial view). —F. Staminode. —G. Pistil. Scale bars equal 10 mm. Drawn from fresh material (Preston 1815 [DAV]).

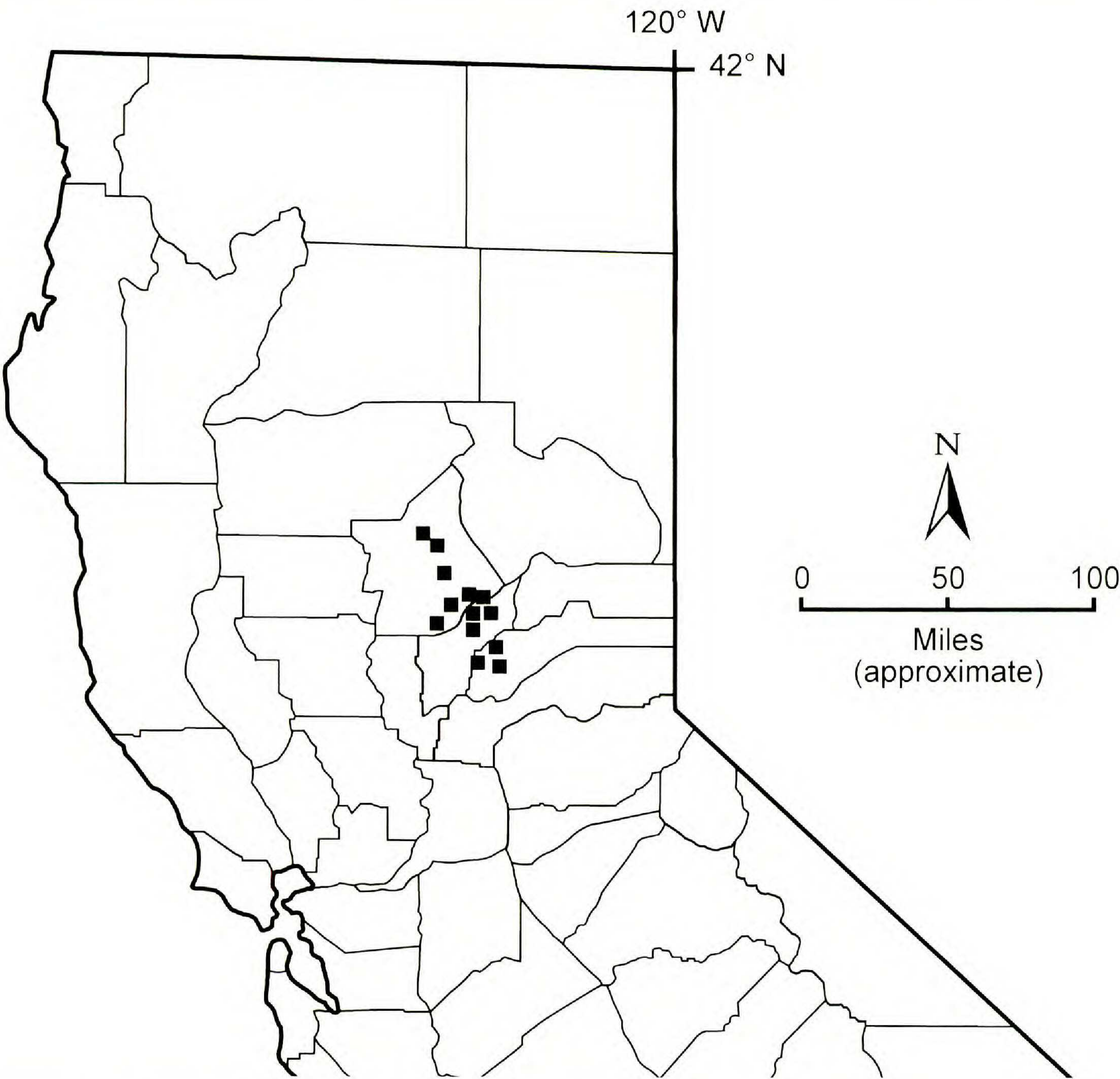


Figure 2. Distribution of *Brodiaea sierrae* (■) in California, U.S.A.

populations occur primarily on soils derived from basic and ultramafic intrusive rocks. Populations of the new species occur on serpentinite outcrops in Butte County near Magalia, Jarbo Gap, and Forbestown. Populations also occur on gabbro outcrops in Butte County near Bloomer Hill and in Nevada County near Grass Valley.

Brodiaea sierrae most commonly grows in chaparral openings but also grows in open areas in foothill woodlands. It rarely occurs in dry meadows. Associated species include *Allium jepsonii* (Traub) S. Denison & McNeal, *Arctostaphylos viscida* Parry, *Brodiaea minor* (Bentham) S. Watson, *Calocedrus decurrens* (Torrey) Florin, *Calochortus superbus* J. T. Howell, *Calycadenia truncata* DC., *Calycadenia multiglandulosa* DC., *Ceanothus cuneatus* (Hooker) Nuttall, *Ceanothus lemmonii* Parry, *Centromadia fitchii* (A. Gray) Greene,

Chlorogalum pomeridianum (DC.) Kunth, *Dichelostemma multiflorum* (Bentham) A. Heller, *Elymus elymoides* (Rafinesque) Swezy, *Eriodictyon californicum* (Hooker & Arnott) Torrey, *Eriogonum umbellatum* Torrey, *Eriophyllum lanatum* (Pursh) J. Forbes, *Gilia capitata* Sims, *Grindelia camporum* Greene, *Heteromeles arbutifolia* (Lindley) M. Roemer, *Monardella villosa* Bentham, *Pinus sabiniana* Douglas, *Pinus ponderosa* C. Lawson, *Quercus douglasii* Hooker & Arnott, *Quercus durata* Jepson, *Quercus wislizenii* A. DC., *Polygala cornuta* Kellogg, *Sanguisorba occidentalis* Nuttall, *Streptanthus polygaloides* A. Gray, *Triteleia bridgesii* (S. Watson) Greene, and *Wyethia bolanderi* (A. Gray) W. A. Weber.

Relationships of Brodiaea sierrae. Morphologically, *B. sierrae* appears to be closely related to *B. californica* and *B. leptandra*. *Brodiaea sierrae*

is similar to *B. californica*, and previous researchers did not recognize the differences between them. *Brodiaea sierrae* is distinguished from *B. californica* by its generally larger flowers (33–53 mm long, vs. 34–44 mm in *B. californica*) and by the staminode morphology. In *B. californica*, the staminodes are recurved from the middle and narrowed at the apex, and the margins are undulate-dentate and one-half involute. In *B. sierrae*, the staminodes are uniformly wide and recurved only at the tip. The staminode margins are entire and only about one-quarter involute. In addition, *B. californica* often has a pair of appendages on the back of the stamens that are an extension of the filament. Hoover (1939: 569) stated that the presence of anther appendages was variable in *B. californica*, suggesting that this was environmentally induced by drought, as he observed appendages in plants during two drought years but did not notice appendages in plants collected during a normal rainfall year nor in plants at higher, less drought-prone elevations. I observed anther appendages at a low frequency (ca. 18% of plants) in almost all *B. californica* populations that I sampled, even during a wetter-than-normal year. However, I did not observe anther appendages in any populations of *B. sierrae*—the higher elevation population that Hoover (1939) cited (Hoover 3620 [GH]) is actually *B. sierrae*—which weakens Hoover’s hypothesis that anther appendages are environmentally induced. *Brodiaea californica* is endemic to the northern Sacramento Valley and adjacent lower Cascade Range foothills in Shasta, Tehama, and Butte Counties in California, between 45 and 335 m elevation (see Niehaus, 1971: fig. 7). It occurs on soils of volcanic origin, primarily in annual grasslands, but also in grassy openings within foothill woodlands. Most populations bloom from late April to late May, although populations at the northern end of the distribution bloom in early June (pers. obs.). Flower color in most populations of *B. californica* is pale blue-violet, although some populations have pale pink to nearly white flowers (Rowntree, 1936). Niehaus (1971) determined *B. californica* and populations of the taxon herein described as *B. sierrae* (e.g., Niehaus 245 [UC], 543 [UC]) to be diploids ($n = 6$).

Brodiaea sierrae is most similar morphologically to *B. leptandra* (= *B. californica* subsp. *leptandra* (Greene) J. C. Pires); both species lack anther appendages and have erect staminodes with entire margins. *Brodiaea sierrae* generally has larger flowers (33–53 mm long, vs. 28–42 mm in *B. leptandra*) with wider perianth lobes (outer lobes 6.5–11 mm, vs. 4–8 mm in *B. leptandra*), and the perianth lobe midribs

are red-violet (vs. green in *B. leptandra* [Doalson, 1999]). *Brodiaea leptandra* is endemic to the North Coast Ranges in Sonoma, Napa, and Lake Counties in California, between 35 and 700 m elevation (see Niehaus, 1971: fig. 7). It occurs in chaparral and openings in lower montane coniferous forest. Populations of *B. leptandra* are in bloom from about mid-June to mid-July (pers. obs.).

Brodiaea species traditionally have been recognized on the basis of discrete differences in the shape of the floral parts, and taxa delineated on the basis of size differences or the relative position of floral parts have historically been treated as varieties or subspecies (e.g., Hoover, 1939). Hoover (1939: 570) considered *B. leptandra* to be only a variety of *B. californica*, stating that there was little morphological difference between *B. leptandra* and *B. californica*, the main difference between the taxa being the presence of vegetative offsets in the former. Because Hoover’s concept of *B. californica* included collections (Elvin 46 [UC], Elvin 50 [UC], MacFadden 12577 [CAS], Eastwood 565 [CAS], Keck 1601 [DS], Heller 8097 [DS, UC], Eastwood 3426 [CAS], Hoover 3620 [GH]) herein referred to *B. sierrae*, it is perhaps unsurprising that he did not distinguish the morphological differences. Niehaus (1971) employed a more modern approach, using multiple data sources, including morphology, anatomy, cytology, flavonoid chemistry, hybridization studies, geography, and ecology, to seek a better understanding of the systematics of *Brodiaea*. Although Niehaus (1971: 30) noted that the perianth segments were narrower in *B. leptandra* than in *B. californica*, he also determined *B. leptandra* to be tetraploid ($n = 12$, based on Niehaus 679 & Niehaus 680 [UC]), and he proposed that *B. leptandra* be recognized at species rank on the basis of morphology, cytology, and geographic distribution. Despite Niehaus’s (1971) precedent using multiple sources of data for determining the ranks of *Brodiaea* taxa, later floristic treatments (Keator, 1993; Kiger et al., 2001; Pires, 2002) followed the more traditional approach and maintained *B. leptandra* at infraspecific rank (although not following it consistently, e.g., accepting Niehaus’ similar proposal to recognize *Brodiaea minor* (Bentham) S. Watson and *Brodiaea purdyi* Eastwood on cytological and ecological grounds at species rank, despite considerable morphological overlap between them, rather than as varieties, as Hoover [1939] did). The degree of differentiation between *B. californica*, *B. leptandra*, and *B. sierrae*, in terms of morphology, cytology, geography, ecology, and phenology, indicates that all three taxa should be recognized at species rank.

The phylogenetic relationship between this group of taxa and other *Brodiaea* species remains poorly

resolved. *Brodiaea californica*, *B. leptandra*, and *B. sierrae* are distinguished from other brodiaeas by the large (3–5 cm long), showy flowers with long (2–3 cm), erect staminodes that are closely appressed to the anthers. Only *Brodiaea elegans* Hoover has flowers of similar size (24–47 mm long), but the staminodes in that species are short (< 15 mm) and distant from the anthers. All other brodiaeas have smaller flowers (15–30 mm long) with short staminodes (10 mm or less) that often lean toward the anthers or are not closely appressed to the anthers. Hoover (1939: 568) grouped *B. californica* (including *B. leptandra*) with *B. appendiculata* Hoover in an informal group Appendiculatae on the basis of shared floral and fruit characters, including a membranous hypanthium that splits open as the capsules mature, anther appendages, and erect staminodes with undulate-dentate margins. Niehaus (1971) proposed that *B. californica* was derived from *B. appendiculata* and, in turn, gave rise to *B. leptandra*. The recognition of *B. sierrae* throws that hypothesis into question. It seems unlikely that *B. leptandra* and *B. sierrae*, which are more similar to each other than to *B. californica*, would both be derived from *B. californica*. *Brodiaea californica* is morphologically intermediate between *B. appendiculata* and *B. sierrae*, having flowers of similar size and shape as *B. sierrae*, but having staminodes with undulate margins and anther appendages like *B. appendiculata*, and it is alternatively possible that *B. californica* was derived via introgression between the latter lineages.

Floral morphology alone appears to have limited usefulness for resolving relationships between and among *Brodiaea* species, partly because herbarium studies have relied on diagnostic floral features that are often obliterated when specimens are pressed and dried, and partly because floral character states have not been subjected to a phylogenetic analysis. Additional data are needed to elucidate the relationship among the members of Appendiculatae (Hoover, 1939) and between this group and the other brodiaeas. Niehaus (1971) recognized the difficulty in relying on morphological data for predicting phylogenies in *Brodiaea* and stressed the need for multiple data sources. Burbanck's (1941) suggestion that cytological studies might shed light on the differences among *Brodiaea* species has not yet been fully followed through on. Molecular data also show promise for resolving relationships among brodiaeas (Pires & Sytsma, 2002).

Etymology. The specific epithet refers to the species' narrow geographic distribution in the northern Sierra Nevada foothills. I suggest Sierra foothills brodiaea as the common name. *Brodiaea sierrae* is the

most showy of all the *Brodiaea* taxa and has been distributed commercially as *B. californica*.

Paratypes. U.S.A. **California:** Butte Co., 1 mi. NE of Magalia, *R. E. Preston* 2260 (DAV); Magalia, along The Skyway, 0.1 mi. N of Coutelenc Road, *R. E. Preston* 1811 (DAV); E of Paradise & Magalia, N of Oroville & Jarbo Gap, *R. A. Schlising* 4574 (CHSC); 0.3 mi. N of Jarbo Gap, *M. S. Taylor* 4749 (CHSC); along Bloomer Hill Road, ca. 15 mi. NE of Oroville, *L. Ahart* 4081 (CHSC); 1.2 mi. W of Hurleton, *R. Bacigalupi* 3752 (JEPS); ca. 1.5 mi. S of Hurleton, *L. Ahart* 8045 (CHSC); Forbestown, *R. E. Preston* 1892 (DAV); 2.5 air mi. NE of Forbestown, *L. Ahart* 5084 (CHSC), 8049 (CHSC, JEPS); Nevada Co., 1.5 mi. SE of Yuba/Nevada Co. line along Highway 20, *T. F. Niehaus* 543 (UC); 8 mi. NW of Rough and Ready, *T. F. Niehaus* 245 (UC); 1 mi. W of Grass Valley, *R. E. Preston* 1815 (DAV); ca. 5 mi. SW of Grass Valley, *L. R. Heckard* 3428 (JEPS); Yuba Co., Brownsville, *R. E. Preston* 1894 (DAV); ca. 3 air mi. SE of Challenge, *L. Ahart* 7826 (CHSC, JEPS); ca. 3/4 mi. SE of Woodleaf, *L. Ahart* 8050 (CHSC); 2 mi. W of Dobbins, *M. A. Elvin* 50 (UC); 0.5 mi. S of Indiana Ranch, *M. A. Elvin* 46 (UC).

KEY TO *BRODIAEA SIERRAE* AND RELATED SPECIES IN CALIFORNIA

- 1a. Staminode margins undulate, 1/2 inrolled, midrib not noticeably thickened; filament apex with linear appendages in all or some of the flowers.
 - 2a. Perianth white to pale violet, lobes ca. 3 times longer than the tube; staminodes reflexed in upper half *B. californica*
 - 2b. Perianth dark violet, lobes ca. 2 times longer than the tube; staminodes erect, straight *B. appendiculata*
- 1b. Staminode margins entire, 1/4 inrolled, midrib noticeably thickened; filament appendages lacking.
 - 3a. Perianth lobes 20–30 mm long, mid-ribs green; staminodes 16–21.5 mm long, styles 15–21 mm long *B. leptandra*
 - 3b. Perianth lobes 25–38 mm long, mid-ribs red-violet; staminodes 20.5–30 mm long, styles 20–31 mm long *B. sierrae*

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